

Growth and ecophysiology of seedlings of *Podocarpus falcatus* in plantations of exotic species and in a natural montane forest in Ethiopia

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Abstract: The potential role of exotic tree plantations in facilitating successional processes on degraded areas was evaluated in southern Ethiopia by comparing seedling characteristics, transpiration and photosynthetic performance of *Podocarpus falcatus* seedlings in *Eucalyptus* plantation, *Pinus* plantation, adjacent natural forest and clear-felled plantation site. *P. falcatus* seedlings exhibited differences in architecture between *Eucalyptus* and *Pinus* plantations. They had higher leaf area, shorter internode length and greater number of lateral branches in *Eucalyptus* plantation. At similar vapor pressure deficit (VPD), *P. falcatus* transpired much less than *E. saligna*, especially at higher VPDs. Analysis of fluorescence parameters in the leaves showed no significant differences in the level of dark-adapted and light-adapted fluorescence yield (F_v/F_m and $\Delta F/F_m$, respectively), electron transport rate (ETR) and non-photochemical quenching (NPQ) among seedlings grown inside plantations and adjacent natural forest, indicating similar photosynthetic performance. Nevertheless, there was evidence of photoinhibition in *P. falcatus* in the clear-felled site which had low fluorescence yield but high values of NPQ as protection from photoamage. The light response curves of ETR, NPQ and $\Delta F/F_m$ showed similar light saturation behavior among the seedlings grown inside plantations and natural forest and suggested a sequence of light-adapted to shade-adapted behavior in Natural forest > *Eucalyptus* plantation > *Pinus* plantation. The results show the structural flexibility, better water-use and adaptability of *P. falcatus* in its use of the understory environment of plantation species.

Keywords: chlorophyll fluorescence; height growth; lateral growth; light response curves; transpiration

Introduction

The development of suitable strategies for forest regeneration is an issue of prime concern in the tropics in general and in Ethiopia in particular. Recent approaches focus on use of plantation systems, especially with fast growing plantation species, that serve to rehabilitate degraded sites. By responding to the huge wood demand in the short-term while addressing long-term ecosystem rehabilitation, tree plantations have become promising management options (Keenan et al. 1997; Lugo 1997; Parrotta et al. 1997; Lemma et al. 2006; Alem et al. 2010). Many previous studies have shown that exotic tree species grown in plantations provide understory environments conducive for regeneration of indigenous species under their canopies, and hence, can catalyze successional processes on degraded areas (Loumeto and Huttel 1997; Parrotta et al. 1997; Senbeta and Teketay 2001; Feyera et al. 2002; Senbeta et al. 2002; Guerrero and Bustamante 2007).

The regeneration of indigenous forest species in plantation forests in Ethiopia, especially in the Munessa-Shashemen forest has been well documented (Senbeta and Teketay 2001; Yirdaw 2001; Feyera et al. 2002; Senbeta et al. 2002; Lemenih et al. 2004; Lemenih and Teketay 2005; Tesfaye and Berhanu 2006; Alem and Woldemariam 2009). Some of these studies have shown that plantation forests support higher regeneration of indigenous species (both in diversity and number of individuals) than the adjacent natural forests (e.g. Yirdaw 2001). Investigations have also been conducted that related regeneration to site conditions, land-use history, age of plantations and availability of seed sources (Senbeta and Teketay 2001; Feyera et al. 2002; Senbeta et al. 2002; Lemenih and Teketay 2005). Moreover, the rest of these studies have also shown that overstory plantation species possess different qualities in facilitating natural regeneration of indigenous plants. For example, Lemenih et al. (2004) and Yirdaw and Luukkanen (2004) reported variation in understory light conditions of forest plantations in the Ethiopian highlands which would cause differences in promoting natural regeneration of indigenous species.

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In general, the focus of the previous studies conducted in Ethiopia has been mainly on the diversity and density of natural regeneration of woody species inside plantation forests. Studies on successional processes such as seedling establishment and growth and on functional traits such as transpiration and photosynthetic performance are still scanty. To facilitate succession inside plantation forests to more natural forests, information on growth and ecophysiology of indigenous species inside plantation forests is required. Such evidence has paramount significance in order to relate plantation conditions, especially understory light regime (Yirdaw and Luukkanen 2004), with seedling characteristics (Wang et al. 2009). This will in turn help develop plantation designs in order to promote the role of plantation species as catalysts of succession (Parrotta et al. 1997) in degraded areas. Light is an important factor that determines growth and survival of plants inside forest plantations (Ostertag et al. 2008). Wang et al. (2009) mentioned light as the most important factor for selection of suitable indigenous species under different plantations.

The rationale for this study is to provide ecophysiological information of tropical forest species to facilitate restoration activities via tree plantations. In this study we assessed ecophysiological and growth responses of an indigenous tree species, *Podocarpus falcatus* (Thunb.) R.Br. ex Mirb., inside plantations of *Eucalyptus saligna* and *Pinus patula*, in an adjacent natural montane forest and a clear-felled and open former plantation site in order to evaluate its establishment characteristics, growth performance and survival strategies. In this study we aimed to answer the following questions: Do *P. falcatus* seedlings differ in growth and photosynthetic responses among plantations and natural forest? How do *P. falcatus* seedlings respond to clear-felling of overstory plantation species? Does rate of transpiration differ between seedlings of *P. falcatus* and *E. saligna* inside *Eucalyptus* plantation?

Materials and methods

Description of study area

The study was conducted in Degaga District of Munessa-Shashemene forest at the eastern escarpment of the Great Rift Valley, southern Ethiopia. This forest is one of the 58 Priority Forest Areas of Ethiopia. It is a dry Afromontane forest located about 250 km south of Addis Ababa at 7°13' N and 38°37' E and covers an altitudinal range between 2,100 and 2,700 m. Soils of the study area are classified as Mollic Nitisols (Fritzsche et al. 2006). The main rainy season extends from mid June to mid October with maximum rainfall occurring between July and August. The mean annual rainfall is about 1,250 mm, and the mean annual temperature ranges between 15°C–20°C.

Munessa-Shashemene forest covers a total area of 98,169 ha out of which 17,223 ha is remnant natural forest and 6,791 ha is exotic tree plantations. The major exotic plantation species are *Cupressus lusitanica*, *Eucalyptus* spp. and *Pinus patula*. For this study two exotic plantation species, *Eucalyptus saligna* and *Pinus patula*, adjacent natural forest and open, recently clear-felled site were chosen. The plantations were 0.5 km apart from each other and the clear-felled site was planted with *E. saligna*. These plantation species were chosen primarily for high natural regeneration of indigenous species especially *P. falcatus* under their canopies (Tadele 2004). Natural forest and open area were included to evaluate the facilitating effect of plantations for the colonization of *P. falcatus* in the degraded area. Characteristics of sampled sites are given in Table 1.

Table 1. Sampled site characteristics (age, leaf area index (LAI), number of individuals ha⁻¹ (density), diameter at breast height (DBH) and silviculture) and size (height and diameter at 30 cm) of sampled *Podocarpus* seedlings at Munessa-Shashemene forest.

Sampled site	Age (years)	LAI	Density	DBH (cm)	Silvicultural treatments	Height (cm)	Diameter (cm)
<i>E. saligna</i>	17	1.72	1012	31	1 st rotation thinned	139	1.6
<i>P. patula</i>	31	2.4	823	33.5	1 st rotation thinned	143	1.6
Natural forest	-	1.8	951*	25*	Disturbance (grazing and selective cutting)	136	1.6
Clear-felled	-	-	-	-	Plantation stand cleared for timber production	134	1.5

*Made for individuals with DBH \geq 10 cm.

Study species

Podocarpus falcatus (hereafter referred to as *Podocarpus*) is commercially valuable timber species and found to grow naturally under tree plantations (Feyera et al. 2002; Lemenih et al. 2004; Tadele 2004). To compare water relation of *Podocarpus* with other woody species, seedlings of *Bersama abyssinica*, *Croton macrostachyus* and *Eucalyptus saligna* were also included in the study. *Podocarpus* is known to be the single most dominant tree species of dry Afromontane forests in Ethiopia (Friis 1992). At Munessa-Shashemene forest, both *Podocarpus* and *Croton* constituted 78–82% of the tree basal area and 37–

55% of the Importance Value Index (IVI) of trees (Tesfaye 2008). Detail descriptions of the species can be found in Tesfaye et al. (2002).

Seedling architecture

Branching and leaf characteristics of *Podocarpus* seedlings were recorded in plantations, natural forest and in the clear-felled area. Twenty seedlings of comparable size (height and stem diameter) per site were chosen for investigation. Seedling height and diameter at 30 cm, branch internode length (the mean distance between two successive branches), number of lateral branches

per main branch, leaf area and leaf dry weight were recorded. Height, diameter at 30 cm and internode length were measured by measuring tape. Healthy and fully expanded leaves were used to determine leaf area. From each sampled leaf 0.25 cm² discs were cut. After drying the discs and the remaining leaves at 80°C for 72 h, the total leaf area was calculated from the known area of the discs, the dry weight of the discs and the total dry weight of the leaves. Specific leaf area (SLA) was calculated as the ratio between leaf area and leaf dry weight (m²·kg⁻¹).

Transpiration

Transpiration measurements were made inside *E. saligna* plantation for three indigenous species (*Podocarpus*, *Bersama* and *Croton*) and one exotic species (*Eucalyptus*). *Podocarpus* seedlings grown inside *P. patula* plantation and adjacent natural forest were also included for comparison purpose among sites. For each species four seedlings were chosen and three fully developed leaves per seedling were used to record the rate of transpiration. Measurements were conducted on the same leaves at 2 h intervals between 7:00 and 17:00 h solar time. Transpiration was determined with a Li-Cor diffusion porometer (Li-Cor, Neb., USA) which also recorded PAR (photosynthetically active radiation) and leaf temperature. Porometer measurements were always performed on both sides of the leaves. Leaf conductance for water vapor was estimated as J_{H_2O}/dN where dN is the difference between partial water-vapor pressure in the leaf air spaces and in the atmosphere, obtained from leaf temperature, assuming water-vapor saturation in the leaf air spaces, and from measurements of air temperature and relative humidity.

Chlorophyll fluorescence of PS II

Chlorophyll a fluorescence was recorded *in situ* with a portable pulse-amplitude modulated photosynthesis yield analyzer (Mini-PAM, Heinz Walz, Effeltrich, Germany) equipped with a standard 2030-B leaf clip holder. Four seedlings of *Podocarpus*, which had approximately the same size, were selected inside each stand to monitor fluorescence parameters. Data were collected on three leaves taken at random from each seedling at 2 h intervals between 7:00 and 17:00 h solar time. The same leaves were used for assessment throughout the day. Potential quantum yield of PS II $((F_m - F_o)/F_m = F_v/F_m)$ was measured following Lüttge et al. (2001) in the early morning and during the day after darkening the leaves for 30 min, where F_o is the minimal fluorescence level of dark-adapted leaves with all PS II reaction centers open, F_m is the maximal fluorescence level with all PS II reaction centers closed, determined by a saturating light pulse at 3,000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on dark-adapted leaves, and F_v is the maximal variable fluorescence level. Effective quantum yield of PS II was calculated as $(F_m - F)/F_m = \Delta F/F_m$ (Genty et al. 1989), where F is the steady-state value of fluorescence of light-adapted leaf and F_m is the maximal fluorescence level in the light-adapted state determined by saturating light pulse at 3,000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ superimposed on the prevailing environmental light flux. Non-photochemical quenching (NPQ) was calculated by Stern-

Volmer equation as $\text{NPQ} = (F_m/F_m') - 1$ (Bilger et al. 1995). Apparent rate of photosynthetic electron transport (ETR) was determined as $\Delta F/F_m' \times \text{PAR} \times 0.5 \times 0.84$, where the factor 0.5 accounts for the excitation of PS II and the factor 0.84 assumes a reflection of 16% PAR at the leaf surface (Schreiber et al. 1994).

Light response curves of yield ($\Delta F/F_m'$), ETR and NPQ were constructed using the light curve programme of the instrument, Mini-PAM. Leaves were irradiated with a series of progressively increased actinic light intensities without prior dark acclimation. The light was provided by the instrument's internal light source. Measurements were obtained over a range of PAR values between 5 and 1525 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and increased in eight steps (5, 100, 150, 250, 350, 500, 750, 1040 and 1525 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at 30 s interval. The measurements were taken on three leaves from four seedlings in each stand.

Data analysis

All statistical analyses were done using SPSS Version 16. Prior to analysis, data were tested for normality using Chi-square goodness of fit. Comparisons of seedlings growth and fluorescence parameters at the various sites were assessed using ANOVA according to general linear model (GLM) procedure. Significant differences at the various sites were found through Tukey's Honestly Significant Difference Test. Deviation of potential quantum yield of photosystem II of 30 min dark-adapted leaves from the optimum value, 0.8 (Demmig and Björkman 1987) was identified using Student's *t*-test. The relationship between VPD and rate of transpiration was established through regression analysis. To all citations of significant differences in the text, differences between means were considered significant when $p < 0.05$.

Results

Seedling architecture

The naturally regenerated *Podocarpus* seedlings generally had smaller values of leaf characteristics, internode length and lateral (secondary) branches in the natural forest than in plantations (Table 2). Leaf dry weights and SLA were not significant ($p = 0.09$) among plantations and adjacent natural forest, whereas, leaf area was significantly ($p < 0.01$) smaller in *pinus* plantation. *Podocarpus* seedlings had significantly longer branch internode length and fewer numbers of lateral branches per main branch ($p < 0.01$) in *Pinus* plantation than in *Eucalyptus* plantation. The results generally implied greater biomass allocation in leaves and/or branches of *Podocarpus* seedlings grown inside *Eucalyptus* plantation, which meant enhanced lateral growth and stem growth in *Eucalyptus* and *Pinus* plantation, respectively.

Transpiration

The effect of vapor pressure deficit (VPD) on the transpiration rate of *Podocarpus* seedlings in relation with other indigenous

species and *E. saligna* is shown in Fig. 1. Transpiration was increased with increasing VPD. However, the magnitude of increase in transpiration with VPD was highest in the plantation species, *E. saligna*. In comparison, water loss through transpiration was lowest and did not increase much with VPD in *Podocarpus* seedlings.

The diurnal transpiration in leaves of *Podocarpus* seedlings ranged between 0.70 and 0.82 mmol H₂O m⁻² s⁻¹ and did not significantly vary ($p > 0.08$) between plantations and adjacent natural forest (Table 3).

Table 2. Seedling characteristics of *Podocarpus* in forest understories and in the clear-felled at Munessa-Shashemene forest

Forest type	Branch internode length (cm)	Number of lateral branches	Specific leaf area (m ² ·kg ⁻¹)	Leaf dry weight (g)	Leaf area (cm ²)
<i>Pinus</i> plantation	12a (1.5)	7.5b (0.21)	7.53a (0.47)	0.049a (0.001)	3.69b (0.3)
<i>Eucalyptus</i> plantation	8.7b (1.0)	9.4a (0.24)	7.66a (0.42)	0.055a (0.003)	4.06a (0.5)
Natural Forest	8.1b (1.1)	6.2bc (0.17)	7.13a (0.40)	0.053a (0.004)	3.92b (0.4)
Clear-felled	8.5b (0.95)	6.0c (0.20)	6.57a (0.41)	0.056a (0.003)	3.68b (0.4)

Note: Mean values (± SE) followed by the same letter within each column are not significantly different at $p < 0.05$ (n=20).

Table 3. Comparison of the mean values (± SE) of transpiration, initial fluorescence (F_o), maximal fluorescence (F_m), ETR and NPQ in leaves (30 min dark-adapted) of *Podocarpus* seedlings in forest understories and in the clear-felled at Munessa-Shashemene forest during the course of a day

Characteristics	Transpiration (mmol H ₂ O·m ⁻² ·s ⁻¹)	F_o	F_m	ETR	NPQ
<i>Pinus</i> plantation	0.82a (0.02)	837a (94.0)	3775b (437.4)	9.49b (0.61)	1.57b (0.082)
<i>Eucalyptus</i> plantation	0.78a (0.01)	745b (70.4)	3824ab (287.9)	8.26b (0.53)	1.33b (0.048)
Natural Forest	0.82a (0.04)	850a (31.2)	4052a (382.0)	8.06b (0.48)	1.03b (0.029)
Clear-felled	0.70b (0.05)	740b (16.2)	2632c (366.8)	29.5a (0.66)	4.07a (0.244)

Mean values followed by the same letter within each column are not significantly different at $p < 0.05$ (n=12)

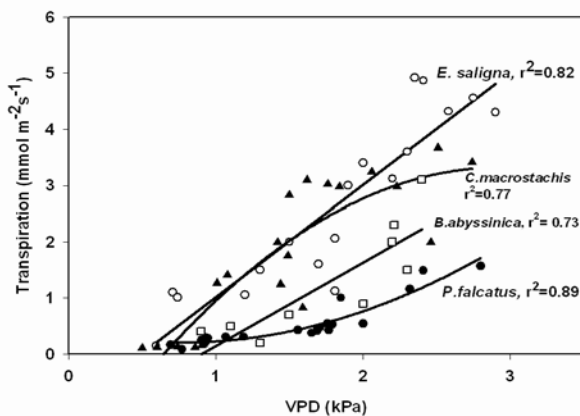


Fig. 1 Relationship between transpiration and diurnal VPD in seedlings of *P. falcatus* (solid circles), *E. saligna* (open circles), *B. abyssinica* (triangles) and *C. macrostachys* (squares) grown inside *E. saligna* plantation at Munessa-Shashemene forest.

Diurnal values of F_v/F_m and $\Delta F/F_m'$: Forest understory versus clear-felled

Chlorophyll fluorescence in the leaves of *Podocarpus* seedlings was measured to evaluate photosynthetic performance in different environments. There was no much difference in chlorophyll fluorescence parameters between the plantations and natural forest, but there were consistent and significant differences ($p < 0.001$) of fluorescence values between the forest understories and

clear-felled area. Potential quantum yield of PS II, F_v/F_m , was around the optimum value, 0.8 (Demmig and Björkman 1987) and almost uniform throughout the day (Fig. 2). Diurnal course of effective quantum yield of PS II, $\Delta F/F_m'$, was minimum close to midday, with a recovery to the early-morning level toward late afternoon (Fig. 3). Interestingly, seedlings in the clear-felled had lower F_v/F_m and $\Delta F/F_m'$ but higher ETR and NPQ values ($p < 0.01$) (Table 3). Furthermore, in the clear-felled, the value of F_v/F_m was below 0.8 ($p < 0.01$) throughout the day.

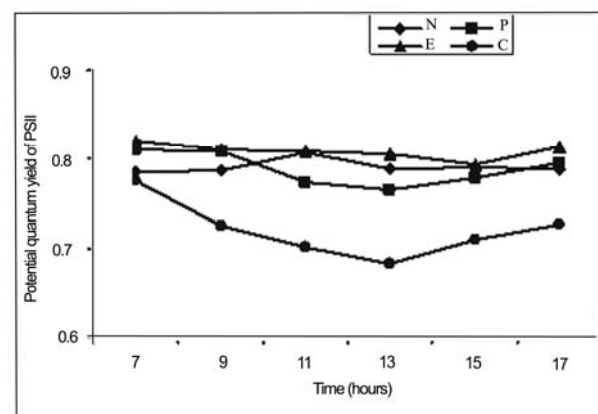


Fig. 2 Diurnal course of potential quantum yield of PS II (F_v/F_m) in the leaves of *Podocarpus* seedlings in the natural forest (N), *Pinus* plantation (P), *Eucalyptus* plantation (E) and clear-felled (C).

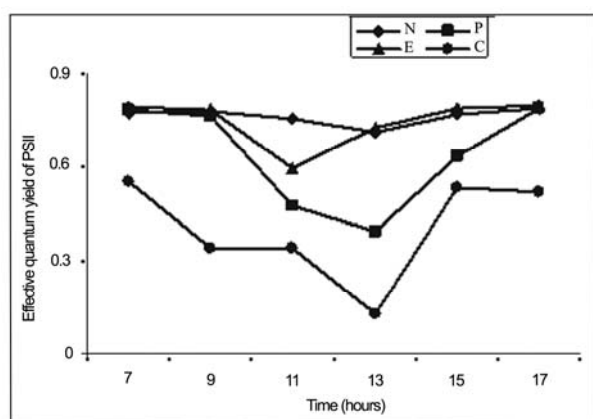


Fig. 3 Diurnal course of effective quantum yield of PS II ($\Delta F/F_m$) in the leaves of *Podocarpus* seedlings in the natural forest (N), *Pinus* plantation (P), *Eucalyptus* plantation (E) and clear-felled (C).

Light response curves: Plantations versus natural forest

Light response curves of non-photochemical quenching (NPQ), electron transport rate (ETR) and effective quantum yield ($\Delta F/F_m$) of *Podocarpus* seedlings grown inside plantations and adjacent natural forest are presented in Fig. 4. With the increase of actinic light, $\Delta F/F_m$ significantly declined while NPQ and ETR increased. The curves of the chlorophyll fluorescence indices were similar across the study sites with ETR being leveled off at high light ($750 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). However, the maximum values of ETR were low in the *Pinus* plantation and high in the natural forest. In the early phases of the light response curves, *Podocarpus* had steeper curves in the *Pinus* plantation. Generally, the curves suggested a sequence of light-adapted to shade-adapted behavior of *Podocarpus* in natural forest > *Eucalyptus* plantation > *Pinus* plantation.

Discussion

Podocarpus seedlings exhibited variation in growth between *Eucalyptus* and *Pinus* plantations. They had broader leaves, higher SLA, shorter internode length and greater number of lateral branches in *Eucalyptus* plantation. This growth pattern of *Podocarpus* seedlings indicates enhanced lateral growth in *Eucalyptus* plantation and height growth in *Pinus* plantation. Lateral growth in *Eucalyptus* plantation helps the seedlings survive in the understory by intercepting much of the available light while height growth in *Pinus* plantation allows them to reach high light levels in the canopy (Kohyama 1987; Kohyama and Hotta 1990; King 1991; Whitmore 1996). Previous studies undertaken in southern Ethiopia showed fewer but bigger individuals of colonizing woody species in *Pinus* plantation than in *Eucalyptus* plantation (Lemenih et al. 2004; Tadele 2004). In a greenhouse study under varied light regimes, Fetene and Feleke (2001) found higher specific leaf area in *Podocarpus* as a strategy to enhance light interception at lower light regimes. Canopy characteristics

(Lemenih et al. 2004; Yirdaw and Luukkanen 2004) certainly influence seedling structure of *Podocarpus* where increase in lateral growth and height growth will be a competitive advantage in the understory in *Eucalyptus* and *Pinus* plantation, respectively. Therefore, silvicultural treatments that create openings are required to enhance growth of established seedlings in *Pinus* plantation.

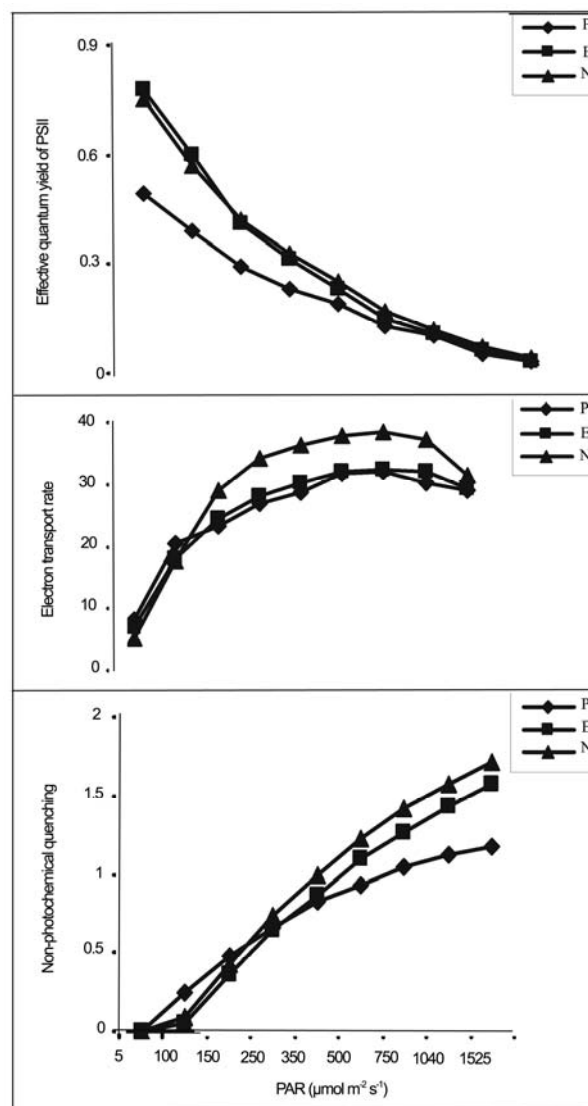


Fig. 4 Light response curves of non-photochemical quenching (NPQ), electron transport rate (ETR) and effective quantum yield ($\Delta F/F_m$) of *Podocarpus* seedlings grown inside natural forest (N), *Pinus* plantation (P) and *Eucalyptus* plantation (E).

Podocarpus had the lowest transpiration compared to other species even at higher VPD (Fig. 1). It is interesting to note that the extent of rise in water loss by transpiration with increasing VPD was considerably higher in *E. saligna*. Under well-watered condition, Gindaba et al. (2004) found higher stomatal conductance and water loss in *E. globulus* and *E. saligna* as compared to three deciduous indigenous trees. These two *Eucalyptus* species were also more vulnerable to induced drought situation than the

indigenous species. Although *Eucalyptus* trees have high water consumption (Florence 1996) which is consistent with the high rate of growth, low transpiration rate of *Podocarpus* indicates its ability to compete well with *Eucalyptus* with respect to water-use. The lower water loss by *Podocarpus* coupled with water absorption of *Eucalyptus* from deep soils and groundwater (White et al. 2000; Burgess et al. 2001) which reduces competition for water shows the possibility to establish mixed plantations of *Eucalyptus* and indigenous species.

Understory light regime in forest plantations exerts considerable effect on understory species richness, seedling recruitment and growth (Parrotta 1995; Ostertag et al. 2008). The values of F_v/F_m and $\Delta F/F_m$ in the leaves of *Podocarpus* seedlings showed that photosynthetic responses of the seedlings were not significant between plantation forests and adjacent natural forest. The variation was, however, significant in the clear-felled where the seedlings were directly exposed to high light conditions. Furthermore, the light response curves of ETR, $\Delta F/F_m$ and NPQ suggested similar light saturation behavior of *Podocarpus* inside plantations and natural forest reflecting that the seedlings were experiencing similar light environment. Plantation forests therefore facilitate growth of established seedlings by stimulating light conditions closely similar to the growing conditions in the natural forests. The canopies of plantation species determine growth of colonizing species by affecting the light environment received at the forest floor. Yang et al. (2009) reported two exotic *Acacia* species to act as nurse plants for understory plants by improving light conditions for photosynthesis. Lemenih et al. (2004) proposed significant influence of canopy characteristics of plantation species on species richness and growth of colonized woody species by affecting light environment at the forest floor. Very interestingly, this study showed that colonizing woody species did not exhibit differences in diameter and height growth between *Pinus* plantations and adjacent natural forests.

Values of potential quantum yield of PS II, F_v/F_m , of normal unstressed leaves is known to be around 0.81 and values below 0.8 generally indicate photoinhibition (reduction in photosynthetic performance) (Björkman 1987). *Podocarpus* seedlings both in the plantations and in the natural forest had F_v/F_m values very close to optimal showing good photosynthetic performance. Nevertheless, in the clear-felled, where *Podocarpus* seedlings were fully exposed to high irradiance, F_v/F_m values (0.71 ± 0.07) were below the optimal range indicating photoinhibition. Similarly, in a previous study *Podocarpus* seedlings grown in full light under greenhouse condition experienced photoinhibition (Fetene and Feleke 2001). The lower F_v/F_m in the clear-felled showed that the seedlings were exposed to some degree of light stress and the protective role of plantation forests from high light stress. On the other hand, these seedlings in the clear-felled had lower F_m and F_o and higher ETR and NPQ values which might indicate the absence of photodamage to PS II (Demmig and Björkman 1987; Demmig-Adams and Adams 1992; Anderson et al. 1997). High levels of ETR and NPQ can therefore be seen as a regulatory response to light stress reducing the probability of photodamage to PS II. The potential of *Podocarpus* to grow in forest understories and in the open area (clear-felled) by protect-

ing its photosynthetic apparatus thus showed its wide ecological tolerance. Dalle and Fetene (2004) and Fetene and Feleke (2001) reported the ability of the species to grow and persist across a wide range of light environments. The species thus offers a wide range of silvicultural options that facilitate natural successional processes inside plantation forests.

Generally *Podocarpus* transpired less amount of water than *Eucalyptus* and performed well photosynthetically inside *Eucalyptus* plantations. The species in the clear-felled, however, showed reduced photosynthetic performance reflecting that canopy plantation species provide light conditions closely similar to that in the adjacent natural forest and protect the indigenous seedlings from high light stress. The regeneration ecology of the species (Fetene and Feleke 2001; Dalle and Fetene 2004) coupled with its ecophysiological responses inside the plantations suggest that degraded *Podocarpus* forests in the highlands of Ethiopian can be restored by integrating *Podocarpus* with *E. saligna*. Understanding germination characteristics and performance of indigenous seedlings in various plantation species, stand densities and moisture regimes is required to promote successional role of tree plantations at degraded areas in Ethiopia.

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